



Kinematic analysis of treadmill locomotion of Tree shrews, *Tupaia glis* (Scandentia: Tupaiidae)

By NADJA SCHILLING and M. S. FISCHER

Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Jena

Receipt of Ms. 05. 08. 1998

Acceptance of Ms. 28. 12. 1998

Abstract

The cineradiographic analysis of the treadmill locomotion of tree shrews, *Tupaia glis* comprises walk, trot, and gallop. At symmetrical gaits, *T. glis* accelerates primarily by increasing step frequency but at gallop, step length is increased by including a suspension period. During all gaits, the site of foot down is directly below the eye. The femur is in horizontal orientation at foot down, at lift off humerus and tibia are parallel to the ground. At the end of the stance phase elbow and knee joint are more extended during symmetrical gaits than at gallop (30–40°). Biphasic shoulder joint movements observable during symmetrical gaits are reduced to monophasic movements at gallop. The onsets of flexion and extension movements are mostly before foot down and lift off. Body propulsion is mainly achieved by action of the proximal limb segments (scapula: 42–43 % during all gaits, ‘pelvic movement’: 42 % at gallop). For the first time, kinematics of the intervertebral thoracic and lumbar joints were calculated from X-ray films. Additive sagittal spine movements occur in the caudad thoracic and lumbar intervertebral joints and contribute substantially to body propulsion. The analysed kinematic and metric parameters of *T. glis* are common in mammals of small to medium size and seem to be independent of the taxonomic group of the animal.

Key words: *Tupaia glis*, cineradiography, kinematics, spine movement

Introduction

Tupaia glis is a small squirrel-like mammal which lives in the tropical and subtropical rain forest of southeast Asia. Tupaiidae are often considered to be a sister group of Primates (NOVACEK 1992). The most recent common ancestor of primates and tupaiaes could have been similar to modern tree shrews as far as anatomy, life history, and locomotion are concerned. Therefore, *Tupaia* could be a “possible ‘model’ of a primitive primate or placental mammal” (JENKINS 1974 a). This idea led to many studies on various aspects of tupaiaid biology, including the first cineradiographic investigations on therian locomotion (JENKINS 1971, 1974 a). JENKINS (1974 a) paid special attention to spinal movements and found the region of greatest sagittal mobility to be located between the four vertebrae Th11–L1. No movements were observed in the lumbar spine.

The observations of JENKINS (1971, 1974 a) were partly in contradiction to our studies on other therian mammals of the same or slightly larger size. We began a series of studies

that centered around the kinematics of taxonomically and morphologically very different small to medium sized mammals. (FISCHER 1994; KÜHNAPFEL 1996; FISCHER and LEHMANN 1998; SCHMIDT and FISCHER 1999). A striking feature in the locomotion of all these mammals was the additive sagittal movement of the lumbar spine during in-phase gaits. Furthermore, body propulsion was mainly achieved by actions of proximal limb segments such as scapula movements.

In this study, the kinematics of fore- and hindlimbs, as well as movements of the complete thoracic and lumbar vertebral column were quantitatively analysed in animals that ran on a treadmill. Kinematics describe the relative orientation of limb segments during a step cycle. It comprise the angular movements in their amplitude and effective contribution to linear step parameters, joint and segment angles at the beginning and the end of stance and swing phase, as well as the intralimb coordination of joint movements. We distinguish between the caudal or cranial rotations of limb segments (i. e., retro- and anteversion, respectively) and the movements of the joints proper. We describe the angles relevant for propulsion in their projection onto the sagittal plane. The kinematics of the intervertebral thoracic and lumbar joints were calculated from X-ray films.

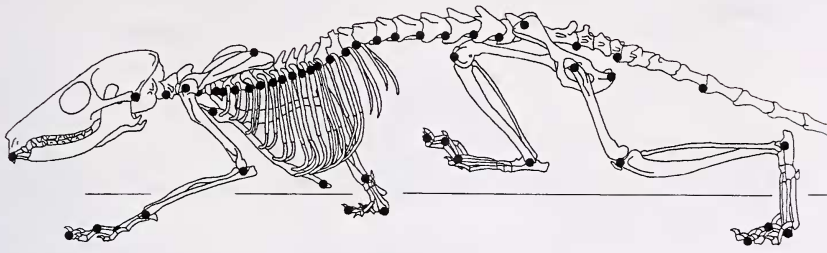
We are especially intrigued about the locomotion of *Tupaia* because of its postulated similarity with, firstly, the most common recent ancestor of primates and, secondly, with that of all placental mammals. In this context the question arises as to whether the characteristics of tupaiid locomotion are strictly size related or show some traits that point to its supposed relationships with primates. We build upon the work of JENKINS, however, our own work on various other mammals showed that a more detailed approach is necessary to address these questions.

Material and methods

Experiments were performed on adult *Tupaia glis*. Only two animals (male 210 g, young female 151 g) could be trained by positive conditioning to move on a horizontal motordriven treadmill within a Perspex® enclosure (100 cm × 45 cm × 11 cm). Tread speed was not fixed, but held manually at a relative constant level during X-ray shots. Only cineradiography allows to track skeletal movements, particularly of the proximal segments, i. e. scapula, humerus, pelvic, and femur. The cineradiographic films were made in several sessions at the Institut für den wissenschaftlichen Film (IWF) at Göttingen. The X-ray system consists of an automatic Phillips® unit with one X-ray source image amplifier chain. Pulsed X-ray shots were applied (50 kV, 200 mA). Films were exposed at 150 frames/s. The animals were filmed in a lateral projection. They were placed as closely to the image amplifier as possible (10 cm) and at maximum distance from the X-ray source (1 m), in order to reduce optical distortions. The images were taken from the image amplifier using a Arritechno® R 35–150 camera. Fore- and hindlimbs were filmed separately because the animal was longer than the X-ray screen (20 cm). An orthogonal grid perpendicular to the projection plane provided reference points for motion analysis and correction of geometrical distortions. The animals were filmed synchronously with two video cameras (50 Hz) in lateral and dorsal views. X-ray films were copied to video tapes (VHS).

In spite of several months of habituation, the tupaia did not perform all possible gaits. The animals did not show bounds on the treadmill. Therefore, only the symmetrical gaits such as walk and trot, as well as gallop were studied. Out of the filmed sequences, for a frame-by-frame analysis only those runs with continuous motion of the animals were selected. The cineradiographic tapes were A–D converted with a video processing board (Screen Machine® I, Fast® Multimedia AG, Munich, Germany). We further processed the frames by using a software that was written for this specific purpose ('Unimark' by R. Voss). It allows to digitize interactively previously defined landmarks with a cursor function, to correct distortions automatically, to calculate angles and distances, and to correct easily erroneously digitized coordinates during analysis. Simple animation tools (stick finger function) of the software help to control data of complete sequences, e. g., to identify and correct confusion of left and right limbs. Skeletal landmarks were captured and their x–y coordinates saved for each frame. The coordinates were used to define vectors and to calculate angles between vectors.

skeletal landmarks



calculated angles

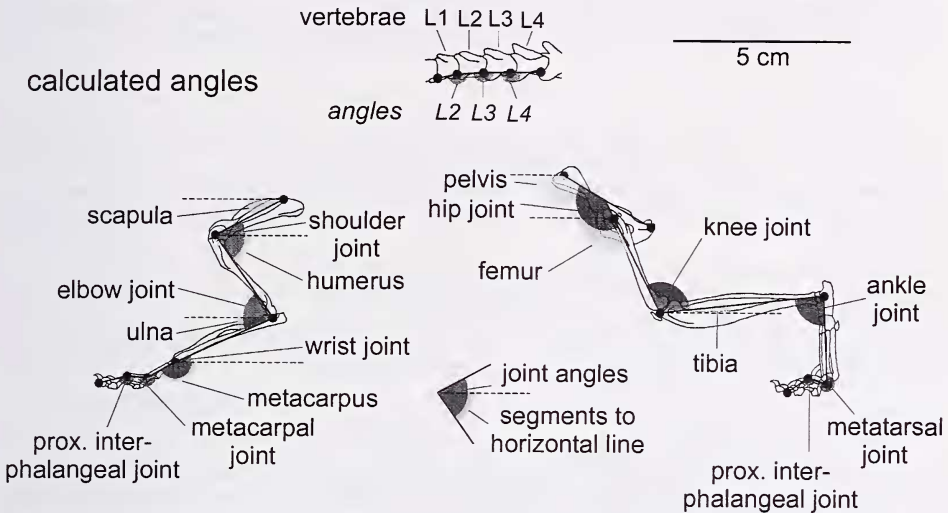


Fig. 1. Skeletal landmarks and calculated angles

Angles were defined anatomically, except for the most proximal ones which were calculated against the horizontal plane. Angle values given in the study represent the projection of the actual angles onto the sagittal plane. The position of digitized landmarks and calculated angles in the parasagittal plane are illustrated in figure 1. Maximum and effective angular movement, timing of segment and limb joint movements and metric gait parameters were analysed. Horizontal and vertical distances, such as the heights of fulcra or step lengths, were measured in cartesian coordinates.

The accuracy of digitization is affected by the contrast of the bones caused by different thickness of proximal and distal body parts. The applied radiation doses were a compromise between the optimal contrast of the proximal and of the distal limb parts. On the same image the most proximal parts are sometimes too dark and the autopodia are too light. The error of landmarks was tested by repeating digitization of five different frames five times. Mean value and standard deviation were calculated for joint angles, segment angles and for x and y coordinates. The average of the standard deviations indicates the digitization error. We estimated digitization errors to be: 1° for elbow, knee and ankle joints, 2° for shoulder and hip joints, 3° for wrist joint as well as 5° for metacarpo- and metatarso-phalangeal joints. The digitization error for the most proximal elements (scapula, pelvis) is lower than 1° . Because of the high frequent undulation of digitization errors of the intervertebral joint movements, those data were analysed by Fourier transformation.

There are different methods to calculate the contribution of movements of a particular limb segment to stance propulsion. FISCHER and LEHMANN (1998) proposed a new approach ('overlay method') for calculating the relative contribution of angular movements, to stance propulsion considering the displacement of fulcra of limb segments.

Calculations are based on mean values of typical gait sequences, of which stance and swing phases are set in the same duration using the method of linear interpolation (Fig. 5, 7) (for details see FISCHER and LEHMANN 1998).

Definitions

touch down: hard contact of foot at the beginning of stance.

lift off: last moment of ground contact at the end of stance.

sequence (one step): from the instance of one foot down to the next foot down of the same foot, including one stance and one swing phase.

scene: film section including several successive sequences.

stride length (s [m]): horizontal distance covered by the trunk or a limb during a one step cycle. It consists of stance length and swing length and is calculated for treadmill analyses by:

$$s = \frac{s_{\text{stance}}}{t_{\text{stance}}} \times t_{\text{swing}} + s_{\text{swing}}$$

stance length (s_{stance} [m]): horizontal distance between the point of foot down and that of lift off, it corresponds to the amount of trunk propulsion in unrestrained locomotion.

swing length (s_{swing} [m]): horizontal distance between the point of lift off and that of foot down.

stride duration (t [s]): period of time from one foot down event to the subsequent foot down event of the same limb.

stance duration (t_{stance} [s]): time period between foot down and lift off of a limb.

swing duration (t_{swing} [s]): time period between lift off and foot down of a limb.

duty factor (D [%]): ratio of stance time to stride duration.

stride frequency (f [s^{-1}]): $1 / \text{stride duration}$.

animal's speed: has to be calculated for the case of treadmill running by:

$$v = \frac{s_{\text{stance}}}{t_{\text{stance}}} + \frac{s_{\text{swing}} - s_{\text{stance}}}{t_{\text{swing}} + t_{\text{stance}}}$$

effective angular movement [$^{\circ}$]: difference between foot down angle and lift off angle.

maximum angular movement (amplitude) [$^{\circ}$]: difference between the maximal and minimal value of angle during the stance or swing phase, respectively.

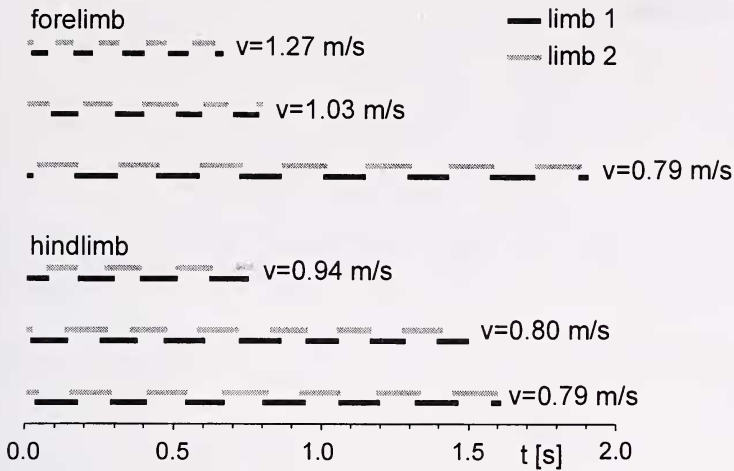
Results

Metric gait parameters (Tab. 1)

The definition of gaits according to HILDEBRAND (1976, 1977) is based on the behaviour of all four limbs during locomotion. For technical reasons we had to record fore- and hindlimbs separately. Therefore, we distinguish between symmetrical (walk, trot) and in-phase gaits (gallop, bound), the latter are defined by an extensive common ground contact interval and a common suspension period. We could hardly distinguish walk from trot, because transitions occurred from one step to another, so they were both included into the category 'symmetrical' gait. All observed in-phase gaits were gallops. The distal elements of the forelimbs were sometimes out of the X-ray screen and only proximal segments could be analysed. Only 6 complete in-phase steps were available for calculating metric parameters. The gait pattern of the analysed cineradiographic scenes are illustrated in Fig. 2.

Forelimb sequences were registered at velocities between 0.54 m/s–1.56 m/s. Symmetrical gaits and in-phase gaits overlap in a range from 0.97 m/s–1.56 m/s. There is no correlation between gait and speed. Hindlimb sequences were recorded at velocities between 0.71 m/s–2.06 m/s. A gap between symmetrical and in-phase gaits was observed at 1.00 m/s–1.32 m/s. Only one step was filmed in this range, at 1.11 m/s.

walk and trot



in-phase gaits

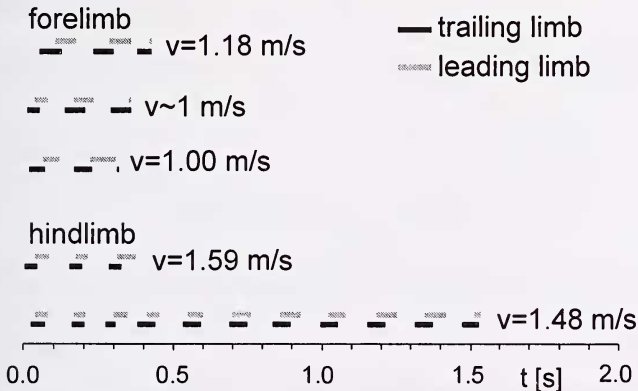


Fig. 2. Footfall pattern of the sequences analysed at different gaits. During in-phase gaits trailing and leading limbs (first and second touching ground) are distinguished.

Stride duration diminishes with increasing speed in symmetrical gaits on fore- and hindlimbs (Fig. 3). Reduction of stride duration is caused by a decrease of stance and swing duration (forelimbs) or stance duration only (hindlimbs). Stance and swing duration were hardly altered at gallop; the resulting stride duration being nearly constant. Speed and stance duration were not correlated on forelimb and on hindlimbs, only swing durations being slightly increased. All duty factors (D) at gallop are less than 50 % on both pairs of limbs. In symmetrical gaits all calculated values account to more than 50 %. With increasing velocity, duty factor decreases.

Forelimb step length slightly decreases with increasing speed at symmetrical gaits caused by decreasing stance and swing lengths (Fig. 4). All limbs travelled longer dis-

a) forelimb

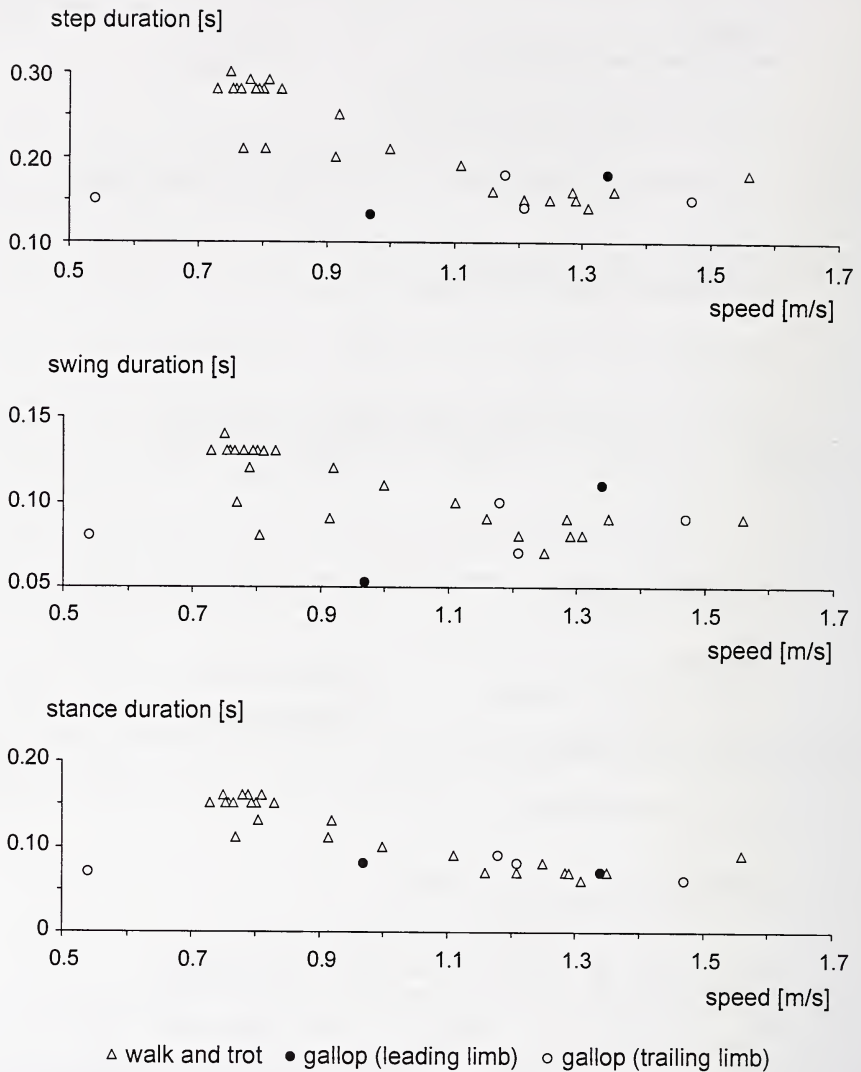


Fig. 3a. Temporal metric gait parameters a) forelimb, b) hindlimb

tances during swing at symmetrical gaits. At gallop, we found a slight decrease in stance length and increase in swing length at higher speeds. On the hindlimb an increase of step length during all gaits is exclusively accounted for increased swing lengths.

Tupaia gains higher speeds by increasing forelimb step frequency in symmetrical gaits. The insufficient data base for in-phase gaits renders it difficult to decide how higher speeds are attained; most probably by an increase of step length. On the hindlimb the animal takes up speed by an increase of swing length in symmetrical gaits and at gallop by longer steps including a suspension period.

The horizontal distances between scapular fulcrum and finger tips (Tab. 2/a) and *Porus acusticus externus* and finger tips (Tab. 2/b) were calculated for analysing the re-

b) hindlimb

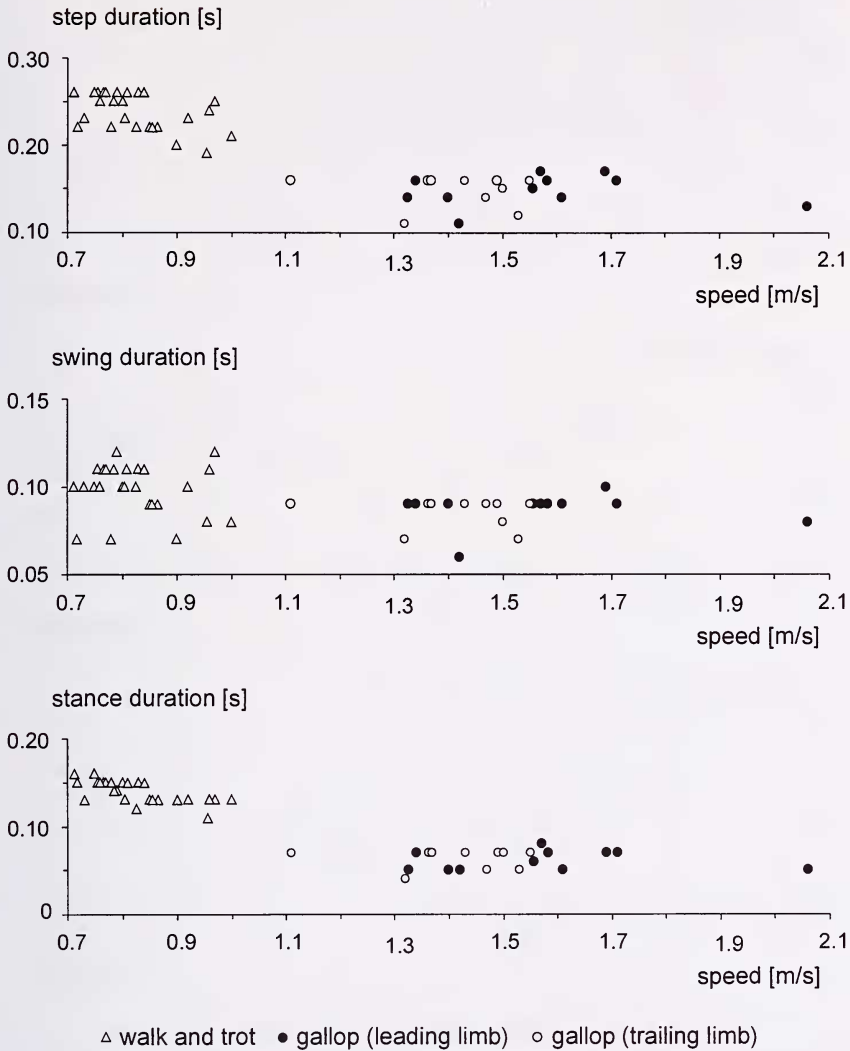


Fig. 3b.

duction of stance length. The latter can be reduced by earlier foot down, lift off or both. The place of foot down is nearly constant at all gaits. Analysed distances between scapular fulcrum and finger tips did not correlate with animal speed or with scapular angle at foot down. However, the extension of the shoulder joint at foot down correlates with this distance during symmetrical gaits. In contrast the shoulder joint is not more extended with greater distances at gallop, but the place of lift off changes with different speeds and gaits. With higher speed, the position of finger tips at lift off is more craniad than at lower speeds. Finally, at gallop the place of lift off lies anterior to the scapular fulcrum. Therefore, stance length is reduced by lift off. The place of foot down is always beneath the eye.

a) forelimb

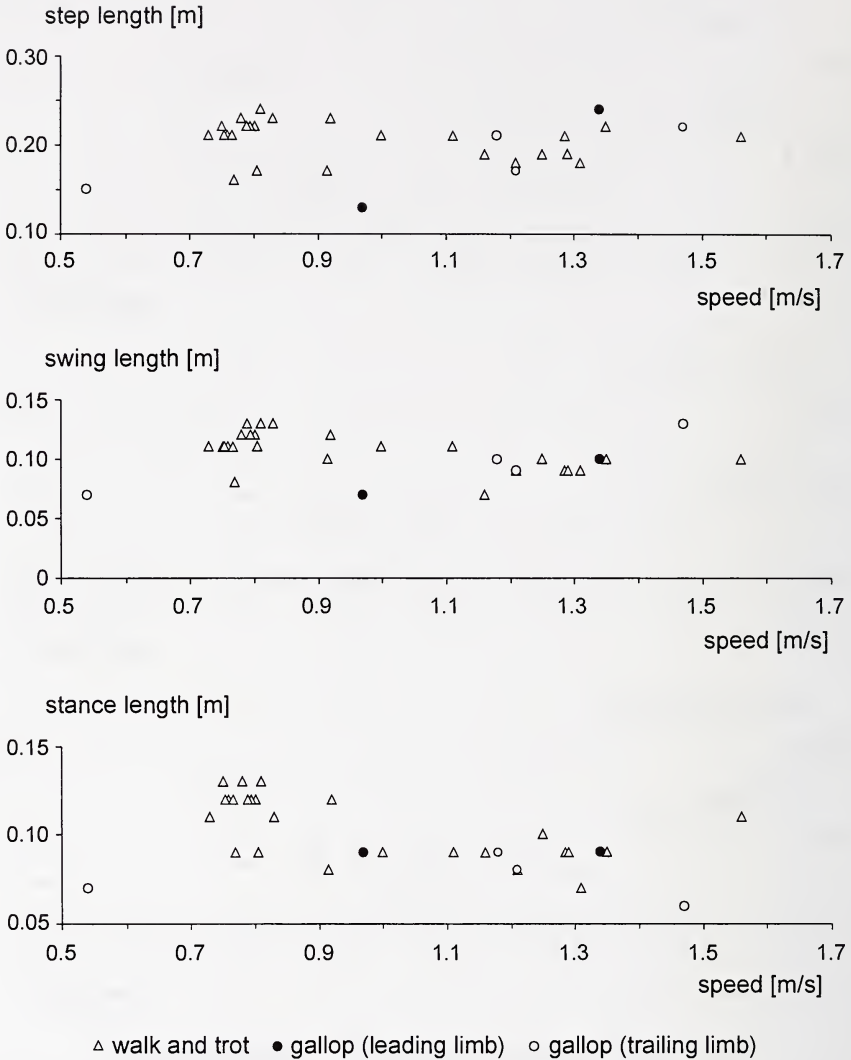


Fig. 4a. Linear metric gait parameters a) forelimb, b) hindlimb

Kinematics

Forelimb (Fig. 5, Tab. 3)

Scapular movements: The point of intersection of the Spina scapulae and Margo vertebralis is assumed to lie close to the scapular fulcrum. Retroversion of the scapula (syn. caudal rotation in FISCHER 1994, or extension in the sense of MILLER and VAN DER MECHÉ 1975; ENGLISH 1978; BOCZEK-FUNCKE et al. 1996) begins with an angle of the scapular spine to the horizontal line of 38° during symmetrical gaits and 45° at gallop. At lift off, this angle amounts to 92° at a walk and trot or 85° at gallop, but its maximal value (90°–

b) hindlimb

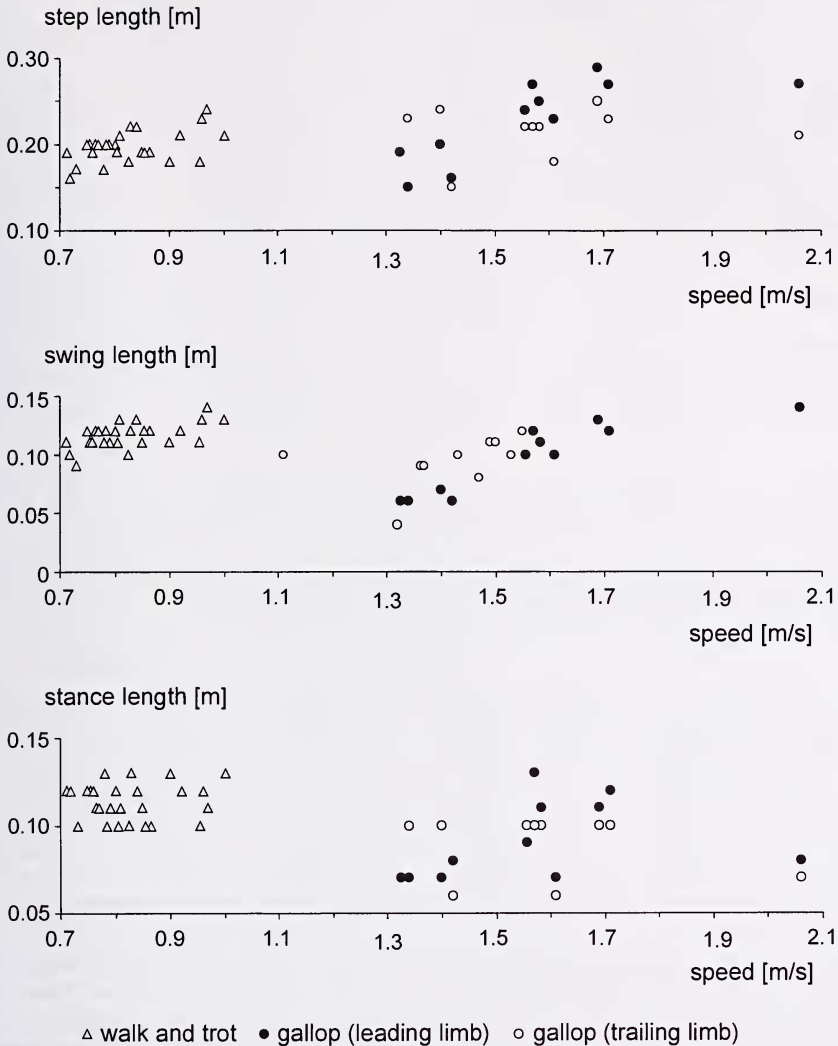


Fig. 4b.

95°) is already reached after 85 % of stance duration. Thus, anteversion sets on before foot up. The scapula follows the shape of the thorax during its cranial movement. As the latter becomes narrower anteriorly, the scapula also moves medially. We could not quantify this movement because of the small size of the animal. The onset of retroversion is after 82 % of swing duration during symmetrical gaits or 74 % at gallop. The smaller amplitude and effective angular movement at gallop is caused by lower cranial and caudal movements. Translation of the scapula in horizontal or vertical direction is small and limited by the clavicle and could not be quantified.

Table 1. Mean values \pm standard deviations (first line) and minimum – maximum (second line) of metric gait parameters.

N	walk and trot		gallop	
	forelimb 25	hindlimb 26	forelimb 6	hindlimb 21
s [m]	0.21 \pm 0.02 (0.16 – 0.24)	0.20 \pm 0.02 (0.16 – 0.24)	0.19 \pm 0.04 (0.13 – 0.24)	0.22 \pm 0.04 (0.15 – 0.29)
S _{stance} [m]	0.10 \pm 0.02 (0.07 – 0.13)	0.11 \pm 0.01 (0.10 – 0.13)	0.08 \pm 0.01 (0.06 – 0.09)	0.09 \pm 0.02 (0.06 – 0.13)
S _{swing} [m]	0.11 \pm 0.02 (0.07 – 0.13)	0.10 \pm 0.01 (0.07 – 0.12)	0.09 \pm 0.02 (0.07 – 0.13)	0.10 \pm 0.03 (0.04 – 0.14)
t [s]	0.23 \pm 0.06 (0.14 – 0.30)	0.24 \pm 0.02 (0.19 – 0.26)	0.16 \pm 0.02 (0.13 – 0.18)	0.15 \pm 0.02 (0.11 – 0.17)
t _{stance} [s]	0.12 \pm 0.04 (0.06 – 0.16)	0.14 \pm 0.01 (0.11 – 0.16)	0.07 \pm 0.01 (0.06 – 0.08)	0.06 \pm 0.01 (0.04 – 0.08)
t _{swing} [s]	0.11 \pm 0.02 (0.07 – 0.14)	0.10 \pm 0.01 (0.07 – 0.12)	0.08 \pm 0.02 (0.05 – 0.11)	0.09 \pm 0.01 (0.07 – 0.10)
D [%]	51 \pm 5 (43 – 57)	59 \pm 4 (52 – 65)	47 \pm 8 (39 – 62)	42 \pm 4 (36 – 47)

Table 2. Mean values \pm standard deviations of the distances between a) scapular fulcrum and finger tips and b) Porus acusticus externus and finger tips at foot down and lift off.

		foot down			lift off	
		N	a [mm]	b [mm]	a [mm]	b [mm]
walk and trot	0.79 m/s	13	69 \pm 3	24 \pm 3	26 \pm 5	96 \pm 4
	1.03 m/s	7	69 \pm 4	24 \pm 4	9 \pm 4	71 \pm 4
	1.27 m/s	8	66 \pm 5	21 \pm 5	5 \pm 5	68 \pm 5
gallop	1.00 m/s	4	50 \pm 8	4 \pm 8	-7 \pm 5	56 \pm 5
	\approx 1 m/s	4	65 \pm 8	17 \pm 8	-4 \pm 4	59 \pm 5
	1.18 m/s	4	72 \pm 5	25 \pm 25	4 \pm 4	66 \pm 8

Shoulder joint: Maximal extension in the shoulder joint was observed after 91 % of swing duration during all gaits. The subsequent flexion begins before foot down, when the shoulder joint angle reaches 123° during symmetrical gaits and 131° at gallop. During symmetrical gaits, it lasts 55 % of stance period, then the following extension continues until very late stance. The angle at lift off is 80°. Lift off is initiated by flexion of the shoulder joint which ends after 37 % of the swing phase. The subsequent extension goes on until shortly before foot down. At gallop, we found a major difference in the scheme of shoulder movement. During the whole stance phase the joint is continuously flexed. The maximum angle occurs at its beginning but the minimum angle (56°) is assumed only at 26 % of the swing phase. So, the extension observed in the second half of stance during symmetrical gaits is lacking at gallop.

Humerus: The humerus has an almost vertical position at foot down (85° at symmetrical gaits and 87° at gallop). During symmetrical gaits, the humerus moves during the subsequent retroversion always over and above its horizontal orientation up to a minimal angle (-19°) after 79 % of stance duration. Until lift off, it is lowered by synchronous extensions in the shoulder and elbow joints (-12°), but immediately afterwards the angle

increases to -22° . Humerus anteversion begins on average after 26 % of the swing phase. The retroversion sets on before foot down with a minimum angle of 99° . In contrast to symmetrical gaits, the humerus is retroverted at gallop during the whole stance phase until 11 % of swing duration to up to -17° . The lift off position is at -13° .

Elbow joint: The elbow joint is flexed starting from a nearly right angle at foot down in the first part of stance (36 % of stance duration at symmetrical gaits, 49 % at gallop). The subsequent extension reaches its maximum (124° at symmetrical gaits, 91° at gallop) at lift off (54 % of steps) or slightly earlier. Flexion reaches its minimum angle of 30° – 40° early in swing (38 % of swing duration) at gallop or at midswing (54 %) during symmetrical gaits. The maximum angle (120° – 128°) is found shortly before foot down (93 % of swing duration). The elbow joint angle at foot up is 30° greater at gallop than during symmetrical gaits and flexion is stronger at foot down during symmetrical gaits. Effective and maximum angular movements at gallop are smaller than during symmetrical gaits.

Lower arm : The lower arm is orientated horizontally at foot down in 78 % of the observations during all gaits. This minimum angle is achieved after 72 % of swing duration. The averaged angles at foot down are 8° during symmetrical gaits and 18° at gallop. Subsequently, retroversion occurs until the end of the stance phase. Angles at lift off are 138° during walk and trot or 105° at gallop. Maximum and effective angular movement are similar during all gaits.

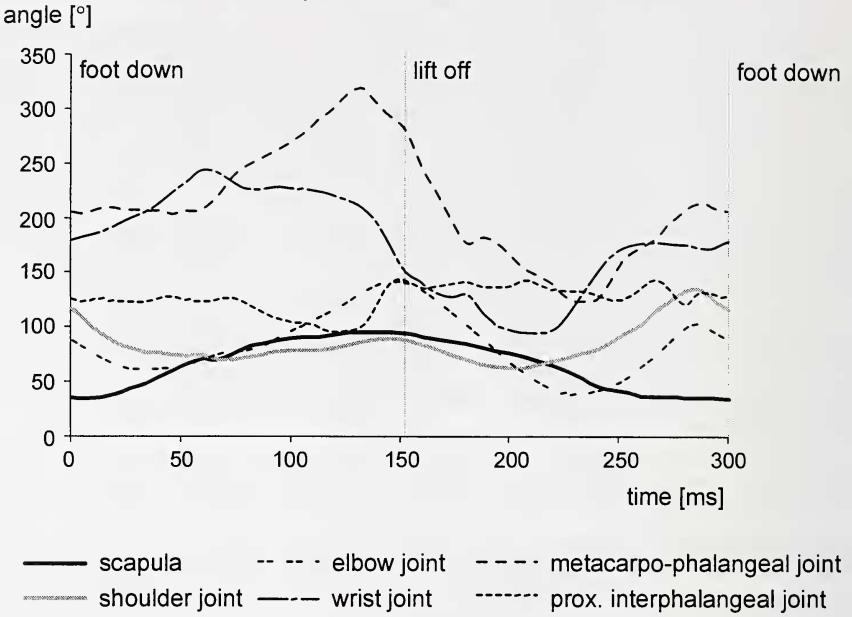
Hand: The hand is placed in a semidigitgrade position, then lowered so that the whole palm is on the ground during all gaits. At midstance, initiated by palmar flexion in the wrist joint, the hand parts are successively lifted off the ground until finally only the tip of the hand maintains ground contact. In the wrist joint, palmar flexion also begins before foot down after 79 % of swing duration, at an angle of 187° during all gaits. Touch down angles amount to 176° during symmetrical gaits and 183° at gallop. During the first half of the stance phase the wrist joint is dorsally flexed up to a maximum of 238° during symmetrical gaits and 223° at gallop. Palmar flexion begins at midstance. After lift off at an angle of 154° during symmetrical gaits or 149° at gallop, palmar flexion continues steadily into the first third of the swing phase (minimum angle of 98° and 107°). No movements occur in the joint between carpus and metacarpus, therefore we regard both elements acting as one segment (hand) during locomotion. Its angle at touch down is between 11° – 18° during all gaits. A minimum angle of -5° is reached after 77 % of the swing phase. The maximum angle of 171° is reached after 10 % of swing duration. Maximum angle and angle at lift off (270° – 290°) in the metacarpo-phalangeal joint were identical in 97 % during all gaits. Minimal angle occurs during swing (109° – 134°) after 46 % of swing duration at all gaits. Angles at foot down are 206° – 222° . Values of the proximal interphalangeal joint scatter largely and are not presented in the tables. During the stance phase, only minor movements are observed. The angle at foot down is about 115° and about 140° at lift off in more than half of the values.

Hindlimb (Fig. 7, Tab. 4): On the hindlimb we distinguish trailing and leading limbs during in-phase gaits. Despite our relatively small sample, we were able to characterize different limb behaviours. The difference at foot down and lift off between both limbs is up to 28 ms ($N = 21$) at an averaged step duration of 150 ms.

Spine movements (Fig. 6): Any small additive vertebral spine movements will result in a displacement of the pelvis because of its immobility in the iliosacral joint. Despite this fact, we call the coupled displacements of pelvis 'pelvic movement' for the sake of simplicity. The angle between pelvis and sacral vertebrae remains constant at 21° during locomotion. During symmetrical gaits, angles in the intervertebral joints from Th3 to L5 are between 170° and 180° ($N = 5$) (Fig. 6) during step. Consequently, 'pelvic movements' are only very small; the difference between the angle at foot down and lift off is only 4° . But at walk and trot two additional 'pelvic movements' were observed. First, a rotation about the dorsoventral axis is discernible, caused by the lateral additive intervertebral joint

forelimb

a) walk and trot



b) gallop

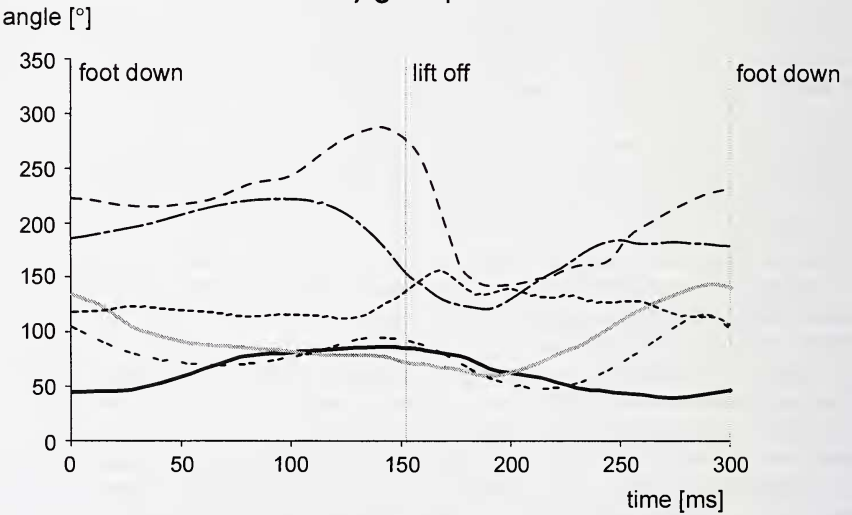


Fig. 5. Scheme of angular movements of forelimb joints a) during symmetrical gaits and b) at gallop

Table 3. Mean values \pm standard deviations of angles at foot down, lift off, minima and maxima in the stance and swing phase of the forelimb (if standard deviation is missing only one value was available).

forelimb	v [m/s] N	walk and trot				gallop	
		0.79 13	1.03 7	1.27 8	≈ 1 4	1.00 4	1.18 4
scapula	down	35 \pm 3	41 \pm 4	39 \pm 6	41 \pm 5	46 \pm 2	48 \pm 9
	lift off	95 \pm 5	89 \pm 5	90 \pm 6	86 \pm 10	86 \pm 1	84 \pm 14
stance	min	34 \pm 3	39 \pm 4	38 \pm 5	39 \pm 5	43 \pm 6	93 \pm 11
	max	97 \pm 5	94 \pm 2	94 \pm 4	90 \pm 6	88 \pm 2	48 \pm 9
swing	min	32 \pm 3	39 \pm 3	36 \pm 4	34 \pm 6	37 \pm 6	39 \pm 5
	max	95 \pm 5	92 \pm 3	90 \pm 6	81 \pm 6	85 \pm 4	82 \pm 15
shoulder joint	down	124 \pm 7	125 \pm 13	120 \pm 12	118 \pm 12	140 \pm 9	136 \pm 13
	lift off	89 \pm 6	74 \pm 8	72 \pm 11	67 \pm 7	76 \pm 5	73 \pm 8
stance	min	67 \pm 4	56 \pm 5	60 \pm 12	67 \pm 7	74 \pm 3	73 \pm 8
	max	124 \pm 7	122 \pm 15	120 \pm 12	118 \pm 12	140 \pm 9	136 \pm 13
swing	min	59 \pm 2	56 \pm 6	48 \pm 6	58 \pm 4	53 \pm 13	57 \pm 7
	max	138 \pm 6	14 \pm 26	134 \pm 10	150 \pm 6	149 \pm 17	144 \pm 15
humerus	down	89 \pm 7	83 \pm 10	81 \pm 12	77 \pm 17	93 \pm 9	88 \pm 13
	lift off	-6 \pm 3	-15 \pm 4	-18 \pm 7	-19 \pm 10	-10 \pm 6	-11 \pm 6
stance	min	-16 \pm 3	-19 \pm 4	-23 \pm 4	-19 \pm 10	-10 \pm 5	-13 \pm 4
	max	89 \pm 7	83 \pm 10	84 \pm 14	77 \pm 17	93 \pm 9	88 \pm 13
swing	min	-18 \pm 3	-23 \pm 1	-28 \pm 3	-23 \pm 6	-14 \pm 11	-15 \pm 7
	max	102 \pm 6	100 \pm 5	95 \pm 8	110 \pm 2	104 \pm 16	99 \pm 8
elbow joint	down	89 \pm 9	92 \pm 10	90 \pm 12	95 \pm 14	113 \pm 13	109 \pm 11
	lift off	139 \pm 10	116 \pm 10	108 \pm 23	83 \pm 20	93 \pm 5	98 \pm 12
stance	min	60 \pm 3	58 \pm 5	59 \pm 4	62 \pm 9	72 \pm 4	72 \pm 3
	max	144 \pm 5	118 \pm 9	113 \pm 22	102 \pm 11	114 \pm 11	113 \pm 8
swing	min	36 \pm 4	27 \pm 5	31 \pm 3	40 \pm 4	47 \pm 14	42 \pm 10
	max	141 \pm 8	119 \pm 6	117 \pm 16	123 \pm 9	123 \pm 24	114 \pm 12
lower arm	down	6 \pm 4	9 \pm 3	9 \pm 6	18 \pm 8	20 \pm 7	21 \pm 4
	lift off	150 \pm 4	131 \pm 7	126 \pm 17	101 \pm 12	103 \pm 6	110 \pm 16
stance	min	6 \pm 4	9 \pm 3	9 \pm 6	17 \pm 8	20 \pm 7	20 \pm 5
	max	151 \pm 4	133 \pm 8	129 \pm 16	103 \pm 11	103 \pm 6	113 \pm 12
swing	min	-3 \pm 4	-3 \pm 3	-4 \pm 3	-6 \pm 5	4 \pm 4	2 \pm 2
	max	150 \pm 4	133 \pm 6	124 \pm 17	101 \pm 12	104 \pm 7	110 \pm 16
wrist joint	down	178 \pm 4	172 \pm 6	176 \pm 5	188 \pm 2	188 \pm 9	184 \pm 3
	lift off	146 \pm 30	158 \pm 14	164 \pm 22	153 \pm 14	157 \pm 15	137 \pm 18
stance	min	143 \pm 29	157 \pm 14	162 \pm 18	226 \pm 5	163 \pm 10	137 \pm 18
	max	248 \pm 5	227 \pm 12	233 \pm 5	153 \pm 14	222 \pm 3	223 \pm 3
swing	min	85 \pm 7	107 \pm 15	111 \pm 9	95	114 \pm 7	111 \pm 7
	max	183 \pm 3	191 \pm 6	191 \pm 5	184	191 \pm 1	188 \pm 3
carpus+	down	11 \pm 3	18 \pm 3	14 \pm 3	15 \pm 1	15 \pm 6	17 \pm 3
metacarpus	lift off	170 \pm 17	153 \pm 12	141 \pm 14	128 \pm 4	126 \pm 12	152 \pm 5
	stance	1 \pm 4	7 \pm 2	7 \pm 7	1 \pm 1	12 \pm 2	10 \pm 3
swing	min	170 \pm 17	153 \pm 12	141 \pm 14	128 \pm 4	126 \pm 12	152 \pm 5
	max	0 \pm 3	-9 \pm 8	-8 \pm 4	-	-6 \pm 7	-1 \pm 3
metacarpophalangeal j.	down	197 \pm 7	172 \pm 6	178 \pm 13	-	149 \pm 18	161 \pm 8
	lift off	206 \pm 10	222 \pm 4	219 \pm 10	221 \pm 2	220 \pm 16	222 \pm 9
stance	min	280 \pm 24	286 \pm 15	289 \pm 11	281 \pm 21	277 \pm 11	273 \pm 13
	max	196 \pm 6	210 \pm 4	210 \pm 5	208 \pm 6	212 \pm 3	211 \pm 5
swing	min	326 \pm 6	304 \pm 9	293 \pm 6	289 \pm 1	284 \pm 9	298 \pm 17
	max	109 \pm 9	124 \pm 9	134 \pm 16	112	132	132 \pm 15
	max	280 \pm 25	289 \pm 14	288 \pm 11	241	244	233 \pm 25

movements ('lateral bending', JENKINS and CAMAZINE 1977). It was estimated using the horizontal distance (x-coordinates) between hip joints in lateral projection. This horizontal distance between hip joints reaches an averaged maximum of 3 mm when foot down

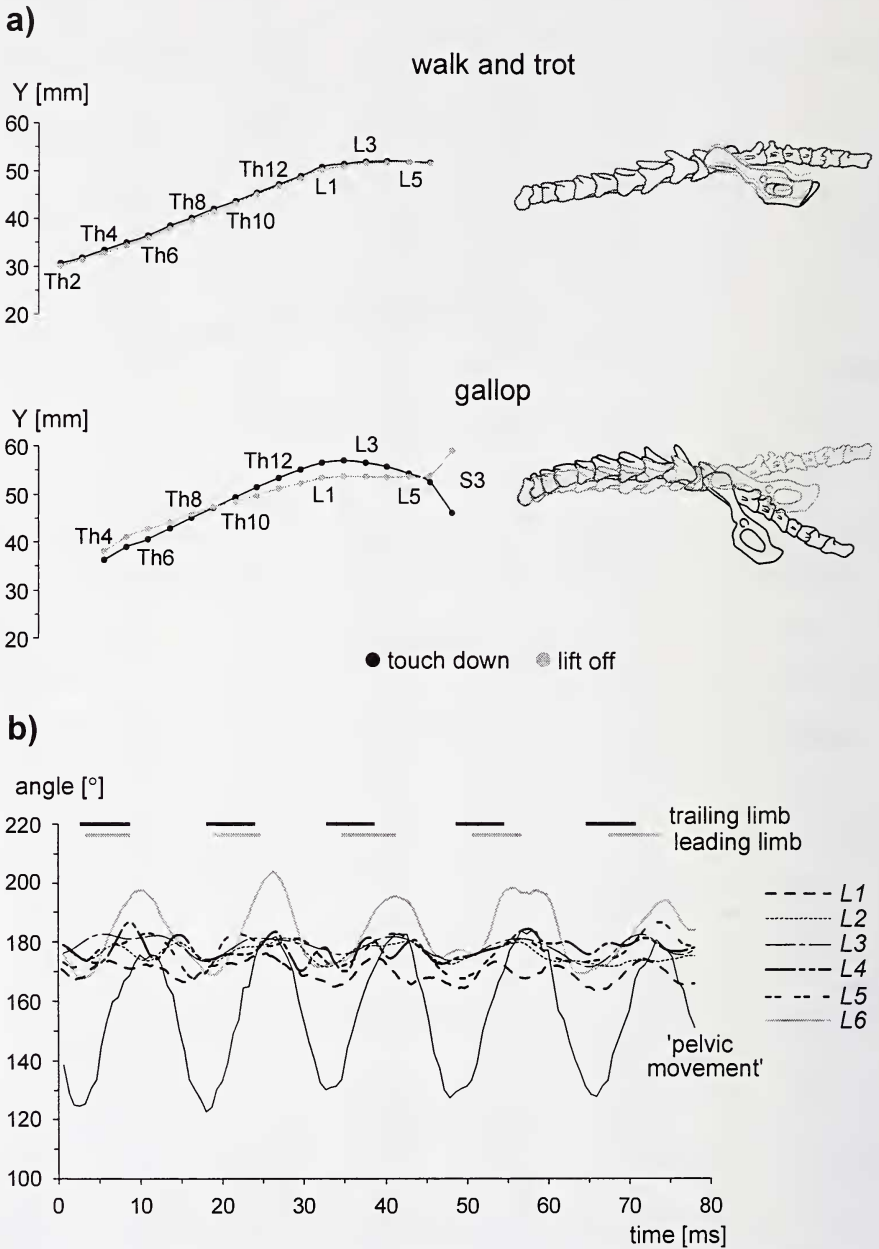


Fig. 6. Sagittal spine movements, a) height of vertebrae over the ground during symmetrical gaits and at gallop; additive sagittal spine movements and resulting 'pelvic movement' at foot down and lift off (for the left foot during symmetrical gaits and for the trailing limb at gallop); b) amplitudes of intervertebral lumbar spine bendings and resulting 'pelvic movements'

takes place on one limb and foot up on the other limb. It corresponds to an angle of approximately 8° of rotation about the dorsoventral axis, with a range of $5\text{--}13^\circ$ during all sequences. The second 'pelvic movement' is a rotation about the longitudinal axis ('tilting', JENKINS and CAMAZINE 1977). It was calculated from the vertical distance (y-coordinates) between both hip joints with up to 5° . At gallop, extensive sagittal 'pelvic movements' occur. Pelvic retroversion begins after 91% (trailing limb) or 79% of leading limb swing duration. It continues into early swing phase before anteversion sets on at 22% of trailing or leading limbs swing phase. Different individuals seem to have different amplitudes at similar speeds (39° at $v = 1.48$ m/s, 28° at $v = 1.59$ m/s) resulting from different angles at foot down (Tab. 4). The cranial angle between the longitudinal axis of the pelvis and the horizontal line (Fig. 1) is up to 12° less in the trailing limb than in the leading limb at foot down. At foot up this difference is $7\text{--}13^\circ$. Maximum amplitudes of trailing and leading limbs are similar at different speeds. Sagittal spine movements are localised in the posterior thoracic and lumbar spine (Th11-L6). The angles for the lumbar intervertebral joints are illustrated in figure 6. Intervertebral movements increase caudad: L1-L4: $8^\circ\text{--}9^\circ$, L5: 13° , L6: 26° . The total excursion of the pelvis is less than the sum of the angles of the single intervertebral joints because the respective angular maximum is achieved successively (43° , $N = 5$). The propagation wave of the extension starts in the thoracic region and runs caudally. Vertebral flexions begin in the caudal thoracic region followed by the lumbar region. The maximum extension in all vertebral joints is found at lift off or shortly thereafter. Anteversion also starts with flexion in the caudal thoracic intervertebral joints.

Hip joint: Hip, knee and ankle joint kinematics are strikingly different during symmetrical gaits and gallop, the amplitude generally being lower at gallop. The amplitude of the hip joint angle during walk and trot is 110° , but at gallop it is less than 70° (Tab. 4). As step length is more or less the same, the reduced angular movements have to be compensated 'pelvic movements'. The higher amplitude during symmetrical gaits is caused by a stronger extension at lift off (141° , as compared to 110° in trailing and 106° in leading limb), and a stronger flexion at foot down (35° at walk and trot, 38° in leading limb and 110° in trailing limb). The hip joint is continuously extended during stance. Flexion of hip joint lasts for more than 80% of swing duration, reaching minimum angles of 28° (walk and trot) or 32° (gallop). The angles at foot down in the trailing limb are greater than in the leading limb. Effective angular movements at gallop are half of the movements that may be observed during symmetrical gaits.

Femur: Hip joint movements, and in the case of gallop also sagittal 'pelvic movements', lead to gait-dependent rotations of the femur. Femur retroversion begins after 90% of swing duration in symmetrical gaits with a minimal angle of 9° below the horizontal line and reaches an angle of 16° at foot down. At gallop ($v = 1.48$ m/s), the timing of the retroversion is similar but the trailing limb femur is kept almost horizontally and one of the leading limbs is even up to 14° above the horizontal line. In the other gallop scene ($v = 1.59$ m/s) both femora do not reach a horizontal position, because the pelvis is less anteriorly displaced (see above). Retroversion ends shortly before or at lift off. Averaged angles at lift off are about 20° higher during symmetrical gaits than at gallop. In the latter, retroversion of the segment continues mostly into early swing phase (about 12% of swing duration).

Knee joint: The amplitude in the knee joint is 72° during symmetrical gaits but only 48° at gallop. While foot down angles are quite similar (Tab. 4), angles at lift off are markedly (by about 30°) smaller at gallop than during symmetrical gaits (124°). Minimal angles (55°) were noticed after the first part of stance during all gaits, when the ankle joint passes beneath the hip joint. Flexion lasts up to 43% of the trailing limb's stance duration or 40% of stance phase of the leading limb and for 27% of the stance phase during symmetrical gaits. During symmetrical gaits, extension is finished in 30% of steps at lift

off, in 10 % one frame (1/150 s) later and in 60 % one frame earlier. At gallop, it coincides with lift off. After 62 % of swing phase a minimal angle of 42° is observed during symmetrical gaits. It is followed by a brief extension until, finally, flexion begins before foot down. Minimal angles (30° – 40°) occur at midstance at gallop.

Tibia/Fibula: The angle of the longitudinal axis of the shank to the horizontal line is 49° at foot down during symmetrical gaits. The lower leg is then retroverted to a minimum angle of -11° after 63 % of stance phase. Until lift off it returns to a horizontal position (-1°). A minimal angle of -18° after 36 % of swing duration is noticed. Anteversion is terminated shortly before foot down (60° after 89 % of swing duration). At gallop, minimum angles are found after 82 % of stance duration in the trailing limb and 76 % in the leading limb. Angles at lift off are smaller in the trailing limb than in the leading limb. Retroversion begins always before foot down in both limbs after 87–88 % of swing duration. The shank is never found in a vertical but always in caudal orientations.

Ankle joint (talocrural joint): Maximum amplitude at gallop is about 30° lower than that at walk or trot (Tab. 4), although angles at foot down are larger (71° as compared to 58°) during symmetrical gaits. At lift off the ankle joint is $>35^\circ$ more extended during symmetrical gaits than at gallop. Initial dorsal flexion is observed at 17 % of the stance phase during these gaits, but significantly later in the trailing limb (38 %) or leading limb (40 %). The succeeding plantar flexion ends slightly before lift off (14 % of steps), at lift off (38 %), or, in 48 % of observations, after 8 % of the swing phase at walk and trot. Plantar flexion of the trailing limb lasts in all sequences into the swing phase, that of the leading limb only in two thirds of steps. In the other cases, plantar flexion of the leading limb ends at lift off. The subsequent dorsal flexion continues for two thirds of the swing phase during all gaits. After a short plantar flexion the dorsal flexion begins, which lasts until stance phase.

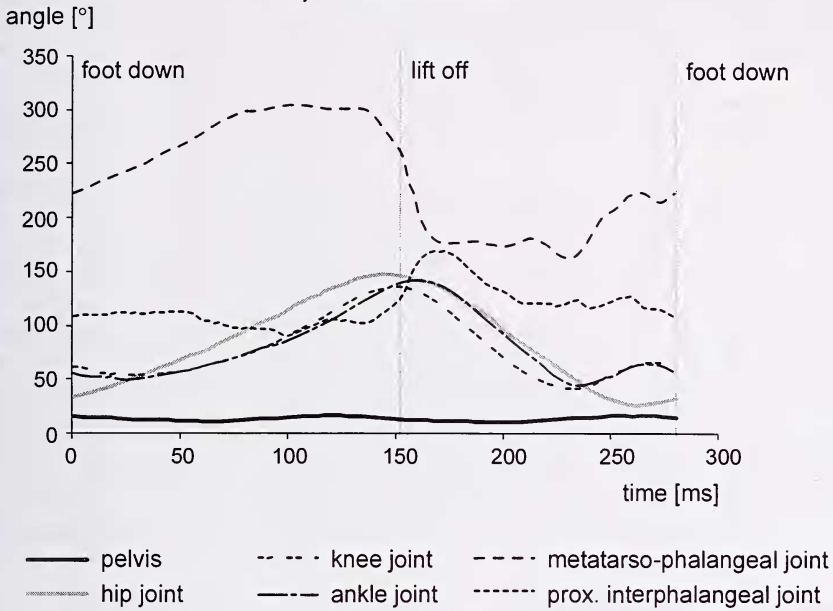
Foot: Six steps were analysed to estimate movements between tarsus and metatarsus. Movements in the tarso-metatarsal joint are found at foot down and immediately afterwards with a dorsal flexion of about 15° . During the remainder of the step we observed an angle of nearly 180° in this joint. Therefore, tarsus and metatarsus were regarded as one segment. Its retroversion begins always just before foot down during walk and trot. After foot down (9°), the retroversion lasts until the end of stance (34 % of steps) or into the swing phase (66 % of observations). Angles at lift off reach 138° . Angles at lift off were smaller at gallop than at walk or trot as a consequence of smaller angles in the talocrural joint. Anteversion ends considerably later than dorsal flexion in the ankle joint at about 85 % of swing.

Metatarso-phalangeal joint: After foot down at an angle of 217° , the joint is dorsally flexed to a maximum of 312° after 74 % of stance duration during symmetrical gaits. Angles at lift off are widely scattered; the averaged angle is 250° . Plantar flexion during swing phase reaches a minimum angle of 156° after one-third of swing duration in 34 % of the steps, or after two-thirds of swing in 66 % of the steps. The subsequent dorsal flexion continues into the stance phase. Joint angles and timing at walk and trot are comparable with those at gallop. In the latter, minimum angles occur earlier (trailing limb after 38 %, and leading limb after 26 % of swing) during the swing phase, and maximum and effective angular movements are smaller. As in the forelimb, the angles of the proximal interphalangeal joint are scattered and not presented in a table. For example, the maximum angle during stance phase is observed in 40 % of observations ($N = 26$) in the first half, in 20 % in the second half of stance, and in 40 % at lift off. The angle at foot down is approximately 110° at walk or trot and about 130° at lift off. The maximum angle is after lift off (average 173°). The leading limb has greater effective angular movements and amplitudes than the trailing limb. Angles of the metatarso-phalangeal joint at foot down and lift off are smaller at gallop than at walk and trot (trailing limb: foot down 110° , lift off 112° ; leading limb: foot down 105° , lift off: 112°).

Intralimb coordination (Fig. 8): Foot down is initiated by palmar flexion of the wrist, followed by scapula retroversion. Just after 90 % of swing duration synchronous flexions in shoulder and elbow joint begin. Coincident with foot down, dorsal flexion during the stance phase starts in the wrist joint. In the first third of stance extension of the elbow joint and at midstance of the shoulder joint follows. Lift off is introduced by wrist joint

hindlimb

a) walk and trot



b) gallop

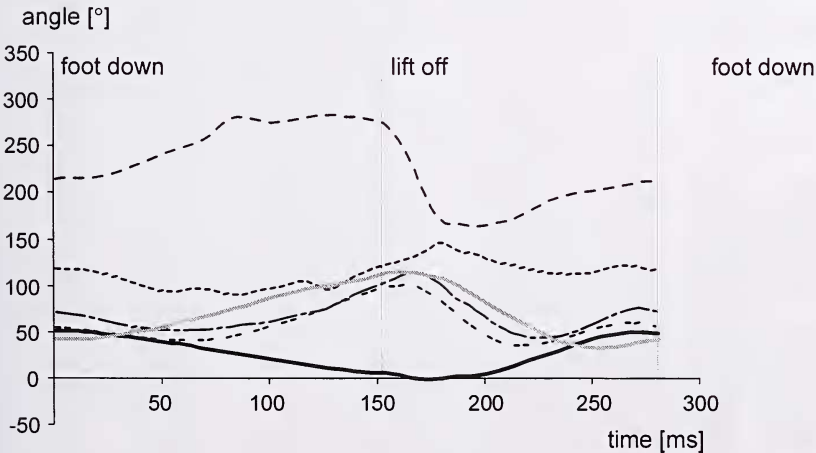


Fig. 7. Scheme of angular movements of hindlimb joints a) during symmetrical gaits and b) at gallop

Table 4. Mean values \pm standard deviations of angles at foot down, lift off, minima and maxima in the stance and swing phase of the hindlimb (if standard deviation is missing only one value was available).

hindlimb	v [m/s] N	walk and trot			gallop			
		0.79 11	0.80 10	0.94 5	1.48 9 trailing	1.59 9 leading	1 trailing	2 leading
pelvis	down	164 \pm 4	159 \pm 7	159 \pm 2	132 \pm 7	137 \pm 8	143	154 \pm 6
	lift off	167 \pm 4	163 \pm 6	163 \pm 5	170 \pm 5	177 \pm 5	169	182 \pm 4
stance	min	161 \pm 3	153 \pm 4	157 \pm 1	131 \pm 6	137 \pm 8	143	154 \pm 6
	max	171 \pm 3	169 \pm 4	166 \pm 4	170 \pm 5	178 \pm 5	169	182 \pm 5
swing	min	161 \pm 3	154 \pm 4	157 \pm 2	131 \pm 7	130 \pm 6	143	143
	max	171 \pm 3	168 \pm 6	164 \pm 4	182 \pm 3	182 \pm 4	182	182
hip joint	down	34 \pm 4	34 \pm 5	42 \pm 5	49 \pm 6	39 \pm 5	55	37 \pm 4
	lift off	145 \pm 5	135 \pm 8	143 \pm 10	113 \pm 13	112 \pm 8	106	100 \pm 18
stance	min	33 \pm 4	33 \pm 5	42 \pm 5	48 \pm 6	39 \pm 5	55	37 \pm 5
	max	149 \pm 4	139 \pm 8	147 \pm 7	113 \pm 13	112 \pm 8	106	100 \pm 18
swing	min	25 \pm 3	28 \pm 4	35 \pm 3	32 \pm 5	33 \pm 3	29	33
	max	146 \pm 5	135 \pm 8	145 \pm 9	115 \pm 14	118 \pm 8	115	101
femur	down	17 \pm 5	13 \pm 7	21 \pm 5	1 \pm 10	-4 \pm 11	18	11 \pm 6
	lift off	132 \pm 7	118 \pm 9	126 \pm 9	103 \pm 16	109 \pm 10	95	108 \pm 22
stance	min	17 \pm 5	13 \pm 7	21 \pm 5	11 \pm 0	-4 \pm 11	18	11 \pm 6
	max	134 \pm 5	120 \pm 6	128 \pm 6	103 \pm 16	109 \pm 10	95	108 \pm 22
swing	min	9 \pm 3	6 \pm 4	14 \pm 4	-6 \pm 10	-14 \pm 7	5	4 \pm 1
	max	132 \pm 7	118 \pm 9	126 \pm 10	111 \pm 14	116 \pm 9	109	113 \pm 14
knee joint	down	62 \pm 4	64 \pm 4	70 \pm 6	58 \pm 7	74 \pm 33	71	75 \pm 11
	lift off	133 \pm 11	112 \pm 13	127 \pm 14	91 \pm 15	87 \pm 20	88	108 \pm 24
stance	min	54 \pm 5	54 \pm 7	58 \pm 4	45 \pm 9	45 \pm 11	55	60 \pm 11
	max	136 \pm 9	115 \pm 10	130 \pm 12	92 \pm 13	104 \pm 15	90	110 \pm 21
swing	min	42 \pm 6	39 \pm 5	47 \pm 7	37 \pm 4	32 \pm 3	41	41 \pm 9
	max	133 \pm 12	112 \pm 13	129 \pm 15	98 \pm 14	112 \pm 13	105	110 \pm 27
shank	down	45 \pm 7	52 \pm 5	49 \pm 7	57 \pm 8	61 \pm 11	55	64 \pm 12
	lift off	1 \pm 5	-5 \pm 6	1 \pm 7	-12 \pm 6	-5 \pm 7	-6	0 \pm 9
stance	min	-11 \pm 4	-12 \pm 6	-7 \pm 3	-15 \pm 7	-10 \pm 7	-6	-6 \pm 12
	max	45 \pm 7	52 \pm 5	49 \pm 7	57 \pm 8	61 \pm 11	55	64 \pm 12
swing	min	-16 \pm 3	-21 \pm 8	-14 \pm 5	-33 \pm 5	-28 \pm 7	-39	-29 \pm 9
	max	56 \pm 4	64 \pm 6	61 \pm 3	71 \pm 7	75 \pm 7	68	81 \pm 7
ankle joint	down	56 \pm 6	57 \pm 6	61 \pm 7	68 \pm 5	71 \pm 10	73	73 \pm 12
	lift off	139 \pm 9	132 \pm 13	140 \pm 7	95 \pm 14	110 \pm 21	100	108 \pm 28
stance	min	49 \pm 5	48 \pm 4	54 \pm 6	54 \pm 6	55 \pm 9	65	59 \pm 4
	max	140 \pm 8	130 \pm 14	141 \pm 6	96 \pm 11	110 \pm 21	100	110 \pm 25
swing	min	42 \pm 6	42 \pm 7	49 \pm 4	38 \pm 4	45 \pm 5	49	48 \pm 18
	max	142 \pm 7	134 \pm 13	141 \pm 7	110 \pm 18	128 \pm 16	107	116 \pm 28
tarsus+	down	12 \pm 3	5 \pm 3	12 \pm 2	11 \pm 4	10 \pm 6	18	9 \pm 8
metatarsu	lift off	138 \pm 6	138 \pm 8	138 \pm 4	108 \pm 17	116 \pm 16	99	109 \pm 24
	stance	min	12 \pm 3	5 \pm 3	12 \pm 2	11 \pm 5	11 \pm 6	17
swing	max	138 \pm 6	138 \pm 8	139 \pm 4	108 \pm 17	116 \pm 16	99	109 \pm 24
	min	6 \pm 3	1 \pm 3	9 \pm 3	-5 \pm 5	-8 \pm 6	10	-4 \pm 9
metatarso	max	143 \pm 5	141 \pm 8	140 \pm 5	125 \pm 16	134 \pm 12	133	121 \pm 7
	down	223 \pm 10	214 \pm 5	212 \pm 5	223 \pm 9	220 \pm 10	227	202 \pm 20
phalang. j.	lift off	262 \pm 25	270 \pm 9	219 \pm 30	275 \pm 12	273 \pm 7	306	243 \pm 20
	stance	min	220 \pm 2	209 \pm 15	203 \pm 14	219 \pm 11	218 \pm 13	227
swing	max	311 \pm 7	312 \pm 3	317 \pm 5	285 \pm 9	289 \pm 7	306	279 \pm 3
	min	155 \pm 10	158 \pm 11	156 \pm 10	154 \pm 11	156 \pm 7	161	152 \pm 6
	max	262 \pm 22	276 \pm 17	236 \pm 17	277 \pm 11	272 \pm 7	306	221 \pm 2

palmar flexion starting already at midstance, followed by scapula anteversion. Flexion in the shoulder and elbow joints coincide with lift off. Extension of the shoulder, elbow and wrist joints begin in the second third of swing phase. Only the shoulder joint shows a strikingly different pattern with gait change. While two flexions and extensions per step were determined during symmetrical gaits, we observed only one flexion and extension per step at gallop. Monophasic extension in the hip joint, flexion of the knee and ankle joints are synchronous and immediately preceding foot down during symmetrical gaits. Additionally, sagittal extensions of the vertebral spine occur at gallop shortly before foot down. Extensions in the knee and ankle joints begin in the first third of stance. Lift off is initiated by a monophasic flexion in the metatarso-phalangeal joint, followed by flexions of the hip and knee joints. The ankle joint flexes dorsally only after lift off. At gallop, the actions of the hip and knee joints are delayed, and start simultaneously with those of the ankle joint after foot up. The onset of anteversion of the pelvis is in the first third of swing phase. The extension in the metatarso-phalangeal joint precedes that of the knee, ankle, and hip joints. With change from walk and trot to gallop shorter flexions in hip and knee joints can be observed.

Body propulsion: The contribution of a limb segment to body propulsion depends on the height of its fulcrum and its effective angular movements. Therefore, the scapula is the main propulsive element in the forelimb during all gaits (42–43 %). For the humerus and the ulna a difference between symmetrical and in-phase gaits occurs. While the humerus contributes only up to 17 % of stance length, it contributes up to 45 % to propulsion at gallop. In contrast, the ulna contributes to propulsion only 3 % at gallop and 32 % at walk and trot. The hand adds 9–10 % of propulsion during all gaits. The contribution of the additive sagittal spine movements to the body propulsion are different between symmetrical and in-phase gaits. At gallop, it amounts to 42 % but at walk and trot only 2 %. Femoral movements account 49 % for propulsion at gallop and 82 % during symmetrical gaits. During all gaits, the shank caused a loss of propulsion (symmetrical gaits: -21 %, gallop: -11 %). The contribution of the whole foot was calculated to be 36 % during symmetrical gaits and 21 % at gallop.

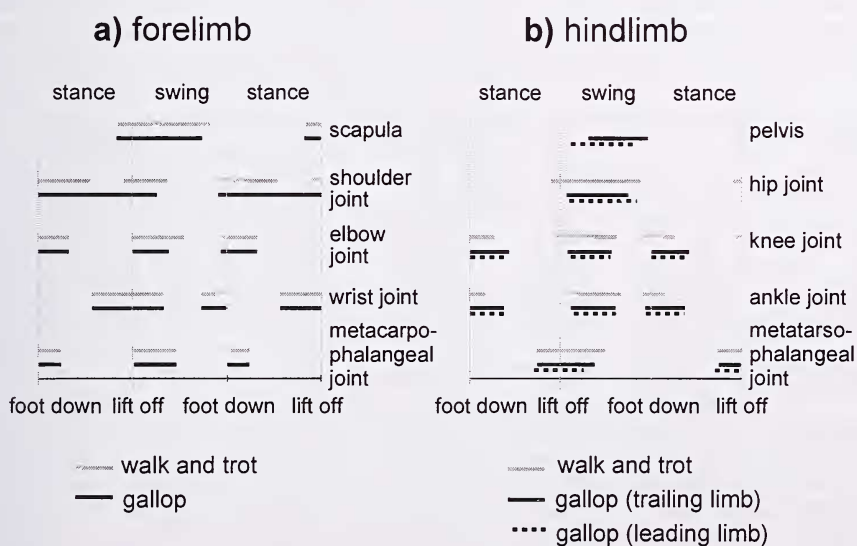


Fig. 8. Intralimb coordination of a) forelimb and b) hindlimb

Heights of the fulcra (Tab. 5): During symmetrical gaits, the most proximal fulcrum on the forelimb (scapular fulcrum) is lower than the hip joint. At gallop, both fulcra are higher than at walk and trot. The scapular fulcrum is situated 43 mm above the ground during symmetrical gaits or 49 mm at gallop: At foot down, the shoulder joint is 32 mm above ground (walk and trot), or 36 mm (gallop). It is lowered down until lift off by 11 mm during symmetrical gaits and 4 mm at gallop. Vertical movement of the elbow joint is higher at gallop (22 mm) than at symmetrical gaits (11 mm). Within a gait, no correlation between those heights and speed are found on the forelimb, whereas on the hindlimb, during symmetrical gaits, the height of the pelvis increases with higher speeds (by 2 mm–4 mm). During symmetrical gaits, constant vertical distances of pelvic and hip joint landmarks above the ground are observed. At gallop, the positions of these points change as a consequence of sagittal spine movements. They are lowered at foot down and rise at lift off. At lift off during walk and trot, the height of the knee joint increases with higher speeds (up to 6 mm) as a consequence of greater extension in the joint.

Table 5. Heights of fulcra of fore- and hindlimb [mm].

forelimb		walk and trot				gallop	
		0.79	1.03	1.27	1.00	≈ 1	1.18
v [m/s]							
N		14	8	9	5	6	6
scapular spine	foot down	44 ± 2	41 ± 3	43 ± 2	51 ± 5	47 ± 4	49 ± 5
	lift off	41 ± 2	41 ± 3	44 ± 2	51 ± 3	48 ± 6	49 ± 5
shoulder joint	foot down	33 ± 1	29 ± 1	31 ± 1	37 ± 5	35 ± 4	37 ± 4
	lift off	18 ± 2	25 ± 3	23 ± 3	33 ± 4	30 ± 4	32 ± 5
elbow joint	foot down	6 ± 1	7 ± 2	6 ± 2	12 ± 3	11 ± 2	12 ± 2
	lift off	22 ± 1	31 ± 3	31 ± 5	38 ± 1	38 ± 3	36 ± 2
wrist joint	foot down	2 ± 0	4 ± 0	3 ± 0	4 ± 1	5 ± 2	4 ± 1
	lift off	8 ± 2	11 ± 1	12 ± 1	12 ± 2	13 ± 2	13 ± 1
metacarpo-phalangeal joint	foot down	1 ± 0	2 ± 0	2 ± 0	2 ± 1	1 ± 0	2 ± 0
	lift off	8 ± 2	7 ± 1	6 ± 2	5 ± 2	6 ± 2	8 ± 1
proximal interphalangeal joint	foot down	2 ± 1	3 ± 0	4 ± 0	3 ± 1	3 ± 0	4 ± 0
	lift off	4 ± 1	4 ± 1	4 ± 1	3 ± 1	4 ± 1	4 ± 1

hindlimb		walk and trot			gallop	
		0.8	0.8	0.97	1.48	1.59
v [m/s]						
N		13	13	7	22	6
Tuber coxae	foot down	53 ± 2	52 ± 1	57 ± 3	57 ± 5	58 ± 3
	lift off	53 ± 2	52 ± 2	56 ± 3	56 ± 4	55 ± 4
Tuber ischiadicum	foot down	45 ± 3	46 ± 2	48 ± 3	35 ± 7	45 ± 4
	lift off	46 ± 3	46 ± 2	48 ± 3	53 ± 5	50 ± 4
hip joint	foot down	47 ± 2	47 ± 1	51 ± 3	42 ± 5	48 ± 3
	lift off	47 ± 2	47 ± 1	51 ± 2	51 ± 8	52 ± 5
knee joint	foot down	38 ± 3	36 ± 3	37 ± 3	43 ± 4	40 ± 3
	lift off	19 ± 3	23 ± 3	25 ± 4	21 ± 4	23 ± 6
ankle joint	foot down	4 ± 1	5 ± 1	6 ± 1	5 ± 2	7 ± 2
	lift off	23 ± 4	22 ± 2	24 ± 3	28 ± 4	25 ± 2
metatarso-phalangeal joint	foot down	2 ± 0	1 ± 1	2 ± 0	1 ± 1	3 ± 1
	lift off	10 ± 4	7 ± 2	9 ± 2	7 ± 4	7 ± 4
proximal interphalangeal joint	foot down	4 ± 0	4 ± 1	4 ± 1	5 ± 1	4 ± 1
	lift off	5 ± 1	4 ± 1	5 ± 2	6 ± 3	5 ± 1

Discussion

On a treadmill, animals perform only a portion of their locomotion repertoire. Treadmill locomotion or restrained locomotion can be different from that on a normal ground (unrestrained locomotion), as described, e.g., in horses (BARREY et al. 1993) and humans (ELLIOT and BLANKSBY 1976). Our present observations of unrestrained locomotion during force plate recordings on *Tupaia glis* at gallop show that the limbs are more extended than on the treadmill, the animal jumps higher and gains longer distances during the swing phase (0.3 m–0.4 m). However, only locomotion on the treadmill allows to analyse kinematics properties using cineradiography, and especially to record series of steps.

JENKINS (1974 a) primarily investigated movements of the distal elements in his study on tree-shrew locomotion. His results were based on a small number of observations. He reported only one value for each of the analysed angles during exploratory activity of the animal. During bounding runs, he analysed only the hindlimbs; no data were given for the forelimbs. Only a detailed analysis of many steps, however, allows to recognise and assess the degree of variability or stereotype of parameters in locomotion. A major deficiency in JENKINS' work (1971, 1974 a) is his neglect of the scapula, which contributes to body propulsion of up to more than 40 % in *T. glis* and more than 60 % in other mammals.

According to JENKINS (1974 a), rhythmic flexions and extensions restricted to the intervertebral articulations between Th11 and L1 occur during exploratory activity and bounding run: "... the lumbar series remains rigid and [does] not contribute to even the most extreme flexion observed". His observations are in sharp contrast to ours on *Tupaia* but also on other small mammals. We found movements in the caudal thoracic spine, but the highest intervertebral amplitudes occur in the lumbar region. The sagittal lumbar spine movements in *Procapra capensis* (FISCHER 1994) and *Ochotona rufescens* (FISCHER and LEHMANN 1998) contribute extensively to body propulsion during in-phase gaits. 'Pelvic movement' during symmetrical gaits in *T. glis* is low compared to other small mammals (*P. capensis* < 20°, FISCHER 1994; *Monodelphis domestica* 9°, unpubl. obs.). Most other studies consider only angles of larger segments of the vertebral column to the horizontal line (e.g., JENKINS 1974 a; HECKNER 1982; HUOV 1987). FISCHER (1994) calculated intervertebral joint angles between reconstructed foot down and lift off positions on freshly dead or anaesthetised animals. The present study is the first cineradiographic analysis that measured sagittal spinal movements in intervertebral joints in animals.

Tupaia is comparable to other small mammals in its limb geometry (FISCHER and LEHMANN 1998). Especially at gallop we found almost right angles in shoulder, elbow, hip, and knee joint. Limb segments that are in horizontal orientation at foot down or lift off may contribute with their whole length to step length. Such a positioning is found in: *Didelphis virginia* (JENKINS 1971), *Rattus norvegicus* (JENKINS 1974 b), *Procapra capensis* (FISCHER 1998), *Ochotona rufescens* (FISCHER and LEHMANN 1998), *Eulemur fulvus* (SCHMIDT and FISCHER 1999) for humerus and tibia at foot up and for femur at foot down. In *T. glis*, the ulna is also nearly parallel to the ground at foot down during symmetrical gaits.

In *Tupaia* and those other animals so far analysed with the 'overlay method' (*O. rufescens*, FISCHER and LEHMANN 1998; *Eulemur fulvus*, SCHMIDT and FISCHER 1999) scapular movements contribute substantially to body propulsion (*T. glis*: 42 %–43 %, *O. rufescens*: 67 %, *E. fulvus*: 63 %). Contribution of the humerus ante- and retroversion is comparable between these animals (*O. rufescens*: 21 %, *E. fulvus*: 31 %). In *T. glis*, the effects of humerus movements are different during symmetrical gaits (17 %) from gallop (45 %). The ulna contributes 32 % to body propulsion because of the large extension in the elbow joint at the end of stance during symmetrical gaits, but only 3 % at gallop. The contribution of the hand is similar during all gaits (9 %) and larger in *Tupaia* than in other ani-

mals (*E. fulvus*: 1%, *O. rufescens*: 3%). In the hindlimb, propulsive effects of the segments change with gaits, caused by the additive sagittal spine movement at gallop. Spinal contribution is low during symmetrical gaits (2%) and high (42%) at gallop. The femur contributes 49% and the foot 21% to propulsion at gallop. The animal loses some stance length through the movements of the tibia. In *O. rufescens*, sagittal spine movements contribute the major component to propulsion (55%–65%) during in-phase gaits, followed by the tibia (19%–35%), femur (8%–10%) and foot (4%–7%).

HEGLUND and TAYLOR (1988) postulated size-related modes of acceleration. Small mammals should increase step frequency and larger animals step length, but step frequency should remain nearly constant even with increasing speed during in-phase gaits. *Tupaia glis* belongs to intermediate forms as well as *Procavia capensis* (FISCHER 1998) and *Eulemur fulvus* (SCHMIDT and FISCHER 1999), which increase both parameters. An increase in step duration and length is reported for *Rattus norvegicus* (COHEN and GANS 1975). Increase of step frequency is attained by abbreviation of the stance phase (hindlimbs of *T. glis*; *E. fulvus*, SCHMIDT and FISCHER 1999; *Loris tardigradus*, *Nycticebus coucang*, DEMES et al. 1990; *Macaca mulatta*, *Felis catus*, humans, VILENSKY and GEHLSSEN 1984), of the swing duration (*Dasyuroides byrnei* at in-phase gaits, KÜHNAPFEL 1996) or both parameters (forelimbs of *T. glis*; *R. norvegicus*, COHEN and GANS 1975; *P. capensis*, FISCHER 1998). JENKINS (1974 a) described a shortening of the stance duration without differences in the footfall pattern during symmetrical gaits ($v = 1.5\text{m/s}$ – 1.75m/s). Swing duration seems to be increased (JENKINS 1974 a), but no details were given. In the present study, a decrease of the stance duration up to 75% was found during symmetrical gaits; at gallop step frequency is almost constant.

All mammals analysed so far have speed independent swing durations (COHEN and GANS 1975; ELLIOT and BLANKSBY 1976; VILENSKY and GEHLSSEN 1984; HOY and ZERNICKE 1985; DEMES et al. 1990; VAN WEEREN et al. 1993; FISCHER 1994; KÜHNAPFEL 1996; SCHMIDT and FISCHER 1999). The measured values for *Tupaia* are in the range of animals of comparable size (70 ms–140 ms).

A remarkable result is the almost constant horizontal distance between the scapular fulcrum and the finger tips at foot down (symmetrical gaits: $68 \pm 4\text{ mm}$, gallop: $62 \pm 7\text{ mm}$). In contrast to this, JENKINS (1974 a) figured foot down beneath the shoulder joint. Such a positioning of the foot seems to be a speciality of exploratory activity, but is never observed at faster gaits. Also in *Monodelphis domestica* and *Dasyuroides byrnei*, the distance between the fulcrum of the scapula and finger tips scatters only slightly (*M. domestica*: $35 \pm 3\text{ mm}$, $N = 34$; *D. byrnei*: 32 ± 5 , $N = 19$; own observ.). Foot down is below the eye point in *T. glis*, *M. domestica*, *D. byrnei* as well as in *Galea musteloides*, *Rattus norvegicus* (unpubl. observ.) and *Ochotona rufescens* (FISCHER and LEHMANN 1998). In contrast, the point of foot down lies in front of the eyes in *Eulemur fulvus* (SCHMIDT and FISCHER 1999) which has elongated limbs.

The onsets of the various flexion and extension movements are not synchronous with foot down and lift off. The movements of nearly all joints on the fore- and hindlimb start before foot down or lift off in *Tupaia glis*. A beginning of scapula retroversion well before foot down was also described for *Procavia capensis* (FISCHER 1994), *Felis catus* (BOCZEK-FUNCKE 1996), *Ochotona rufescens* (FISCHER and LEHMANN 1998), *Eulemur fulvus* (SCHMIDT and FISCHER 1999), *Dasyuroides byrnei*, *Monodelphis domestica* (unpubl. observ.). In contrast, anteversion of the scapula begins at different times e.g., in the last quarter of stance (*T. glis*, *E. fulvus*, *F. catus*, *M. domestica*) or at lift off (*P. capensis*, *Cercopithecus aethiops* (WHITEHEAD and LARSON 1994)). Retroversion before foot down could reduce deceleration forces (FISCHER 1994). Measurements of ground reaction forces prove that deceleration forces in *T. glis* are relatively small (unpubl. observ.).

For the first time, a gait-dependent kinematic behaviour of a limb joint is observed. During symmetrical gaits, the shoulder joint movements in *Tupaia* comprise two flexions

and two extensions per step. Only one flexion and one extension occur at gallop. With change of gaits, shoulder joint movements are reduced from a biphasic to a monophasic pattern.

The works of WHITEHEAD and LARSON (1990) and SCHMIDT and FISCHER (1999) are the only cineradiographic studies on primate locomotion (*Cercopithecus aethiops* and *Eulemur fulvus*, respectively) available at present. Shoulder joint amplitudes are significantly larger in the terrestrial *C. aethiops* than in small non-primates. A remarkable scapular movement was described for *E. fulvus*, including a distinct mediad rotation. Both species as well as other primates have elongated limbs. *Tupaia glis* does not share these features with primates. The locomotion of *T. glis* is similar to that of other small mammals in its kinematic and metric parameters. It appears that these parameters are common in mammals of a small to medium size class, independent of their taxonomic group.

In all analysed small to medium-sized mammals body propulsion is mainly achieved by actions of the proximal limb segments. The flexed limb posture enables the animal to react to obstacles and reduce vertical displacement of the centre of gravity. The horizontal orientation of the upper arm and lower leg at lift off, and the upper leg at foot down seem to be standard parameters of the locomotion of small mammals. Additive sagittal spine movements contribute substantially to body propulsion during in-phase gaits. All these features probably occurred in the most recent common ancestor of therian mammals.

Acknowledgements

We are indebted to Prof. Dr. H.-R. DUNCKER (Gießen) and Prof. Dr. H.-J. KUHN (Göttingen) for kindly providing us with the animals. We thank Dr. D. HAARHAUS and his staff (IWF Göttingen) for their patience and competence in cineradiography. We also thank all members of our working group in Jena for many discussions, and especially Dr. A. HAAS (Jena) and PD Dipl. Ing. Dr. Med. H. WITTE (Jena) for thoroughly revising the manuscript. M. ROSER (Jena) skilfully helped with the illustrations. This research was supported by the Deutsche Forschungsgemeinschaft (DFG) (Fi 410/1-3; Innovationskolleg "Bewegungssysteme", Teilprojekt B 1).

Zusammenfassung

Kinematische Analyse der Fortbewegung von Tupaia glis (Scandentia: Tupaiidae) auf dem Laufband

Mit Hilfe der Röntgenkinematographie wurde die Fortbewegung von *Tupaia glis* auf dem Laufband in verschiedenen Gangarten (Schritt, Trab und Galopp) untersucht. *T. glis* erhöht seine Geschwindigkeit in den symmetrischen Gangarten (Schritt, Trab) durch eine Steigerung der Schrittfrequenz, im Galopp wird durch eine Flugphase Schrittlänge gewonnen. Die Vorderextremität fußt in allen Gangarten unter dem Auge auf, der Abfußpunkt liegt in den symmetrischen Gangarten hinter und im Galopp meist vor dem Lot des Scapula-Drehpunktes. Humerus und Tibia werden beim Abfüßen in allen Gangarten horizontal positioniert. Beim Auffußen wird das Femur parallel zum Untergrund gestellt. Die proximalen Extremitätenabschnitte sind maßgeblich am Rumpfvortrieb beteiligt (Scapula in allen Gangarten: 42–43 %, Femur in den symmetrischen Gangarten: 82 % und im Galopp: 49 %). Im Galopp trägt die additive Sagittalbewegung 42 % zum Vortrieb des Körpers bei. Ellbogen- und Kniegelenk werden in den symmetrischen Gangarten am Ende der Stemmphase deutlich weiter geöffnet (30–40°) als im Galopp. Erstmals konnte ein von der Gangart abhängiger Ablauf der Gelenkbewegungen beobachtet werden. Der biphasische Bewegungsablauf des Schultergelenkes mit zwei Beugungen und Streckungen pro Schrittzzyklus in den symmetrischen Gangarten wird auf einen monophasischen Ablauf im Galopp reduziert. Die Dorsal- und Ventralflexionen der Wirbelsäule wurden zum ersten Mal auf der Basis der Röntgenkinematographie untersucht und dabei nachgewiesen, daß es sich im Unterschied zu der bei anderen Säugetieren beschriebenen additiven Lumbalbewegung bei

T. glis um eine additive Thorako-Lumbalbewegung handelt. Die untersuchten kinematischen und metrischen Parameter von *T. glis* stimmen in wesentlichen Punkten mit denen anderer kleiner und mittelgroßer Säugetiere überein. Die Kinematik ist abhängig von der Körpergröße und unabhängig von der systematischen Stellung der Tiere.

Literature

- BARREY, E.; GALLOUX, P.; VALETTE, J. P.; AUVINET, B.; WOLTER, R. (1993): Stride characteristics of overground versus treadmill locomotion. *Acta Anat.* **146**, 90–94.
- BOCZEK-FUNCKE, A.; KUHTZ-BUSCHBECK, J. P.; ILLERT, M. (1996): Kinematic analysis of the cat shoulder girdle during treadmill locomotion: an X-ray study. *Eur. J. Neurosci.* **8**, 261–272.
- COHEN, A. H.; GANS, C. (1975): Muscle activity in rat locomotion: movement analysis and electromyography of the flexors and extensors of the elbow. *J. Morph.* **146**, 177–196.
- DEMES, B.; JUNGERS, W. L.; NIESCHALK, U. (1990): Size- and speed-related aspects of quadrupedal walking in slender and slow lorises. In: Gravity, posture, and locomotion in primates. Ed. by F. K. JOUFFROY, M. H. STACK and D. NIEMITZ. Firenze: Sedicesimo. Pp. 175–197.
- ELLIOTT, B. C.; BLANKSBY, B. A. (1976): A cinematographic analysis of overground and treadmill running by males and females. *Med. Sci. Sports.* **8**, 84–87.
- ENGLISH, A. W. (1978): Functional analysis of the shoulder girdle of cats during locomotion. *J. Morph.* **156**, 279–292.
- FISCHER, M. S. (1998): Die Lokomotion von *Procavia capensis* (Mammalia: Hyracoidea). Ein Beitrag zur Evolution des Bewegungssystems der Säugetiere. *Verhdl. naturwiss. Verein Hamburg (NF)* **32**, 1–207.
- FISCHER, M. S. (1994): Crouched posture and high fulcrum, a principle in the locomotion of small mammals: The example of the rock hyrax (*Procavia capensis*) (Mammalia: Hyracoidea). *J. Hum. Evol.* **26**, 501–524.
- FISCHER, M. S.; LEHMANN, R. (1998): Application of cineradiography for the metric and kinematic study of in-phase gaits during locomotion of the pika (*Ochotona rufescens*, Mammalia: Lagomorpha). *Zoology* **101**, 148–173.
- HECKNER, U. (1982): Vergleichende Untersuchungen des Bewegungsverhalten einiger ursprünglicher Ruminantia. *Zool. Anz.* **209**, 283–293.
- HEGLUND, N. C.; TAYLOR, C. R. (1988): Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. exp. Biol.* **138**, 301–318.
- HILDEBRAND, M. (1976): Analysis of tetrapod gaits: general consideration and symmetrical gaits. In: Neural control of locomotion (Advances in behavioural biology). Ed. by R. M. HERMAN, S., GRILLNER, P. S. G. STEIN, and D. G. STUART. New York, London: Plenum Press. **18**, 191–203.
- HILDEBRAND, M. (1977): Analysis of asymmetrical gaits. *J. Mammalogy* **58**, 131–156.
- HOY, M. G.; ZERNICKE, R. F. (1985): Modulation of limb dynamics in the swing phase of locomotion. *J. Biomechanics* **18**, 49–60.
- HUROV, J. (1987): Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). *Am. J. Primatol.* **13**, 297–311.
- JENKINS, F. A. Jr. (1971): Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and other non-cursorial mammals. *J. Zool. (London)* **165**, 303–315.
- JENKINS, F. A. Jr. (1974 a): Tree shrew locomotion and the origins of primate arborealism. In: Primate Locomotion. Ed. by F. A. Jr. JENKINS. New York: Academic Press. Pp. 85–115.
- JENKINS, F. A. Jr. (1974 b): The movement of the shoulder in clavicate and aclavicate mammals. *J. Morph.* **144**, 71–83.
- JENKINS, F. A. Jr.; CAMAZINE, S. M. (1977): Hip structure and locomotion in ambulatory and cursorial carnivores. *J. Zool. (London)* **181**, 351–370.
- KÜHNAPFEL, M. (1996): Röntgenkinematographische Untersuchungen der Lokomotion von *Dasyuroides byrnei* und *Monodelphis domestica* (Metatheria). Diss. thesis Univ. Tübingen.
- MILLER, S.; MECHE, F. G. A. VAN DER (1975): Movements of the forelimbs of the cat during stepping on a treadmill. *Brain Res.* **91**, 255–270.
- NOVACEK, M. J. (1992): Mammalian phylogeny: shaking the tree. *Nature*, **356**, 121–125.
- SCHMIDT, M.; FISCHER, M. S. (1999): Cineradiographic study of forelimb movements during quadrupedal walking in the Brown Lemur (*Eulemur fulvus*, Primates: Lemuridae). *Amer. J. Phys. Anthropol.* (in press.).

- VAN WEEREN, P. R.; VAN DEN BOGERT, A. J.; BACK, W.; BRUIN, G.; BARNEVELD, A. (1993): Kinematics of standardbred trotter measured at 6, 7, 8, and 9 m/s on a treadmill, before and after 5 months of preface training. *Acta Anat.* **146**, 154–161.
- VILENSKY, J. A.; GEHLSSEN, G. (1984): Temporal gait parameters in humans and quadrupeds: How do they change with speed? *J. Hum. Mov. Stud.* **10**, 175–188.
- WHITEHEAD, P. F.; LARSON, S. G. (1994): Shoulder motion during quadrupedal walking in *Cercopithecus aethiops*: Integration of cineradiographic and electromyographic data. *J. Hum. Evol.* **26**, 525–544.

Authors' address: Dipl. biol. NADJA SCHILLING and Prof. Dr. MARTIN S. FISCHER, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743 Jena, Germany.